A comparative analysis of patterns of recent extinction in birds and mammals

by

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Abstract

Exploring past extinction patterns among taxa can inform us about risks facing currently threatened taxa if such extinctions have been non-random with respect to phylogeny and/or geographical patterns. This study analyses patterns of recent extinctions among birds and mammals in order to determine factors influencing these patterns and whether these factors differed between the two groups. Data on bird and mammal species that have become extinct since 1500, including their distributions and body-masses, were collected from diverse sources. GIS mapping was used to determine spatial patterns of species extinctions. The body-mass distributions of extinct species were also compared with body-mass distributions of samples of extant species. Patterns of extinction were found to differ geographically among birds and mammals. However, underlying factors influencing these patterns were found to be similar, with species endemism being an important predictor of recent extinctions. Recently extinct species were larger, on average, than extant species in both birds and mammals pointing to the influence of human over-exploitation in the extinctions. Invasive species, particularly mammals such as rats, were also an important driver, influencing species extinctions by preying on native birds and competing with native mammals of similar biology. These findings can most likely be extrapolated to reptiles, whose extinctions have been similarly influenced by invasive mammals but not necessarily to amphibians whose recent extinctions and declines are being driven primarily by a complex interaction of factors including emerging infectious diseases.

Keywords: extinction, birds, mammals, distribution, body size.

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Chapter 1: Introduction

Extinction is a natural phenomenon and an integral part of evolution. The estimated cumulative rate of extinction over evolutionary time has been placed at 99.9% of all species that have ever lived (Raup, 1992). Most of these extinctions (90-96%) occurred outside the five major mass extinctions in the planet's history, marking the end of the Ordovician, Devonian, Permian, Triassic and Cretaceous periods (Raup, *op cit.*). Despite this high proportion of species losses, the rate of "background" species extinctions (i.e., extinctions outside of the five mass events) is estimated at 1-10 species per year (May *et al.*, 1995). The current human-induced extinction of species differs from the natural, background rate of extinction in being more persistent and widespread than past events (Aitken, 1998). There is a growing body of evidence suggesting that rates at which species are becoming extinct is comparable to extinction rates during the five mass extinctions (May *et al.*, 1995; Pimm *et al.*, 1995; Myers & Knoll, 2001).

Current rates of extinction (based on birds and mammals which are relatively well-studied taxa - Soulé, 1990) are estimated to be 100-1000 times higher than the natural background extinction rate (Pimm *et al.*, 1995). Scientists argue that the earth is entering a sixth mass (anthropogenic-induced) extinction phase (Leakey & Lewis, 1995 in Avise *et al.*, 2008). There is thus a need to investigate patterns of recent species loss and assess how these can inform us about the extinction risks facing currently threatened species.

Patterns of avian diversity, richness, and current threat

Bird species are unevenly distributed across families. For example, over 5000 species of the close to 10 000 described species are passerines (IUCN, 2008). Avian species

richness also differs geographically. Highest species densities occur in tropical areas, decreasing with increasing latitude (Gaston, 2000). Predictors of species richness have been found to vary depending on the scale studied. At the regional or continental scale, habitat heterogeneity and energy availability influence species richness (e.g., Allen *et al.,* 2002; Turner & Hawkins, 2004). At the global scale, however, models predict topographic variability and temperature to be the most important predictors of species richness (Davies *et al.,* 2007).

Birds are the best-documented taxa on the IUCN red list (Butchart *et al.,* 2006). Since 1500, 134 species of birds are thought to have become extinct, and 1226 species (or one in eight of all known species) are threatened with extinction to varying degrees (BirdLife International, 2008). The majority of avian extinctions (90%) have been of insular species despite the fact that most bird species have continental distributions (Johnson & Strattersfield, 1990). Rates of avian extinction since 1500 may be 30-300 times higher than the background extinction rate (e.g., Butchart *et al.,* 2006). More recently (since 1900) avian extinction rates have been 57-570 times higher than the background extinction rate (Butchart *et al., op cit.*), indicating that extinction rates are accelerating.

Thirteen families of birds have been disproportionately affected by recent extinctions. Among these, the Anatidae (ducks, geese and swans), Rallidae (rails and crakes), Psittacidae (parrots) and Sturnidae (starlings) have suffered a disproportionately high rate of extinctions. The Dromaiidae (emus), Raphidae (Dodo *Raphus cucullatus* and solitaires) and Acanthisittidae (New Zealand wrens) have all lost 50% or more of their species in the last 500 years. Among the families that have suffered significantly fewer extinctions than expected by chance alone are the Accipitridae (hawks and eagles),

Formicariidae (ant-thrushes), Furnariidae (ovenbirds), Tyrannidae (tyrant-flycatchers), Muscicapidae (thrushes, babblers, warblers and Old World flycatchers) and Emberizidae (buntings) (BirdLife International, 2008). Current threats also impact avian taxa disproportionately, with albatrosses, cranes, parrots, pheasants and pigeons facing the highest levels of threat – 82%, 60%, 27%, 23% and 20% of species, respectively (BirdLife International, 2008).

Habitat loss, invasive species impacts and over-exploitation have been identified as the most important factors precipitating post-1500 avian extinctions (Bibby, 1994). During the 20th Century, the importance of over-exploitation as a cause of extinction decreased, while the importance of habitat loss and invasive species increased over the same period (Butchart *et al.,* 2006). Alien invasive species, including associated introduced diseases, have played an important role and are still expected to be a significant driver of future extinctions (Blackburn *et al.,* 2004, Butchart *et al.,* 2006).

Patterns of mammalian diversity, richness and current threat

The most current compilation of mammal species recognised 5,339 extant species of mammals (Wilson & Reeder, 2005) although an additional 82 species had been described between 1 January 2004 when the compilation went into press and 1 July 2006 illustrating that mammal discovery, description and re-description are on-going (Reeder *et al.,* 2007). Studies of mammalian diversity and endemism have identified basic dispersion patterns linked to biogeography and ecology as well as historical and evolutionary influences (Ceballos & Brown, 1995). As in birds, species richness in mammals is greater on continental landmasses than on islands (Ceballos & Brown *op. cit.).*

Estimated rates of mammalian extinctions in the past 500 years have placed them at 36-78 times higher than the background rate of the last 65 million years (Regan *et al.*, 2001). Like avian extinctions, most recent mammal extinctions have occurred on islands and have affected certain orders disproportionately (e.g., Rodentia - Ceballos & Brown, 1995.). However, geographical patterns of mammalian species richness and endemism do not correspond with patterns of recent or current threat (Ceballos and Brown *op. cit.*). This pattern was attributed to: a) most recent mammalian extinctions having occurred on islands, b) a lack of adequate information to ascertain extinction status, and c) an emphasis on large and charismatic mammals and a neglect of smaller mammals such as rodents.

This study investigates avian and mammalian extinction patterns since 1500 A.D. The study will attempt to provide a broad level classification of extinction patterns at the level of realms, biomes and at a regional level. The study compares these patterns among birds and mammals and attempts to determine which factors have influenced recent extinction patterns and what commonalities exist among the drivers of extinctions in birds and mammals.

Key Questions

Are there commonalities in spatial patterns of extinction among birds and mammals at a global, biome and regional scale?

Have there been commonalities in temporal patterns of recent avian and mammalian extinctions?

Are there commonalities in the biological drivers of extinctions among birds and mammals?

Can patterns of recent mammalian and avian extinctions inform us about likely risks facing less well-known taxa such as reptiles and amphibians?

Hypotheses

Species endemism was an important predictor of recent extinction patterns in both birds and mammals.

Body size was in important factor in determining recent patterns of extinction in both birds and mammals with larger species more likely to suffer extinction than smaller species.

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Chapter 2: Methods

Data collection

Data on recent mammal and bird extinctions were extracted from two databases as well as from the published literature. For mammals, species identity, taxonomic affiliation, estimated extinction date and former distribution were taken from the American Museum of Natural History's Committee on Recently Extinct Organisms (CREO) database of recently extinct mammals (http://creo.amnh.org).

The CREO database contains data on 61 mammal species confirmed as having become extinct recently, 42 of these since 1500. The criteria used for analysing the extinctions are as follows:

> A claim of species extinction must have been made in order for the species to be considered in the analysis. The taxonomic validity of the species has been determined. The date of extinction has been determined not to predate 1500. If the species is known from live specimens, the documentation of survey efforts must be assessed and their adequacy in establishing absence of the species in its known areas of occurrence determined. If the species is known only from fossil or sub-fossil remains, the fossils can be verified simply by the lack of any other recorded evidence since the dating of the remains. Evidence of biological threats to the species prior to extinction is not proof of extinction but may provide evidence that helps to understand factors leading to the demise of the species.

Data on body-masses were obtained from the published literature (Appendix 1). Data were obtained for the extinct species where available. Where not available, body-masses

of either congeners or of members of a closely related family were used. Where a range of body-mass values was given, the mean of the values was used as the species' body-mass (Appendix 2).

Data on recently extinct birds were obtained from BirdLife International (2008), updated on www.birdlife.org. BirdLife International's database contains data on 134 bird species extinctions since 1500. IUCN (2001) criteria used to assign extinction status are as follows: 1) There is no reasonable doubt that the last individual has died; 2) Exhaustive surveys have been carried out in its known or expected habitat and at appropriate times (diurnal, seasonal and annual) throughout its historical range and failed to record an individual; and 3) These surveys must have been conducted over a time frame appropriate to the taxon's life cycle or life form.

Species identity, taxonomic affiliation and former distribution were obtained from the BirdLife International database. For estimated extinction dates, I used data from a study by Pimm *et al*. (2006) on human impacts on avian extinction rates (data available at: http://www.pnas.org/content/103/29/10941/suppl/DC1). Body-masses were obtained from Dunning (1993) where available. Where not available, Dunning (*op.cit*) was used to obtain masses of all extant members of the same genus and the average body-mass of the genus used for the species in question (Appendix 3).

GIS Analysis

A GIS layer of the Terrestrial Ecoregions Base Global Dataset (Olson *et al*. 2001) was downloaded from the World Wide Fund for Nature's (WWF) website: http://www.worldwildlife.org/science/data/item1874.html. The central coordinates of each species' type locality were obtained using Google Earth (earth.google.com) to

locate the area and the coordinates imported into ArcviewGIS 3.3 as a database file (dbf). The dbf file was overlaid on a WWF Terrestrial Ecoregions shapefile to determine which WWF realms and WWF biomes had experienced the greatest numbers of extinctions in total and by century from 1500 A.D. The map was also used to extract information about extinction patterns at a regional scale. First, extinctions were grouped according to country of occurrence. Island nations located in the same geographical area and with similar patterns of endemism were grouped together. Mauritius and Réunion were grouped together as the Mascarene Islands. The Cayman Islands, the Bahamas, Cuba, Dominica, Hispaniola, Jamaica, St. Lucia, Guadeloupe, Puerto Rico, Martinique and Honduras were grouped together under the Caribbean Islands. The Pacific region included Melanesia (New Guinea, New Caledonia, Vanuatu, Fiji and the Solomon Islands), Micronesia (the Marianas, Guam, Wake Island, Palau and the Caroline Islands), and Polynesia (French Polynesia, Hawaii, Samoa, the Cook Islands but excluding New Zealand). Larger countries such as Australia and the U.S.A. were not grouped with neighbouring states (although their definition included surrounding islands such as Australia's Lord Howe Island).

Statistical analysis

Statistical analyses were performed using Microsoft Excel (1997-2003) and Statistica version 8 (2007). Pivot charts were created of the number of extinctions of both birds and mammals occurring at intervals of 50 years from 1500-2000. A chart was also created of the extinctions in each WWF biome as a percentage of the total number of extinctions in each taxon. Frequency distributions of the body-masses of extinct species of birds and mammals were also compared with frequency distributions of a global sample of bird body-mass distributions (Figure 1 in Blackburn & Gaston, 1994) and two

continental samples of mammal body-mass distributions (Figure 1 in Brown & Nicoletto, 1991; Figure 1 in Bakker & Kelt, 2000).

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Chapter 3: Results

Trends in species extinctions since 1500 A.D.

134 species of birds and 42 species of mammals became extinct between 1500 and 2000. The peaks for bird and mammal species extinctions were between the late 1800s and early 1900s (Fig. 1).

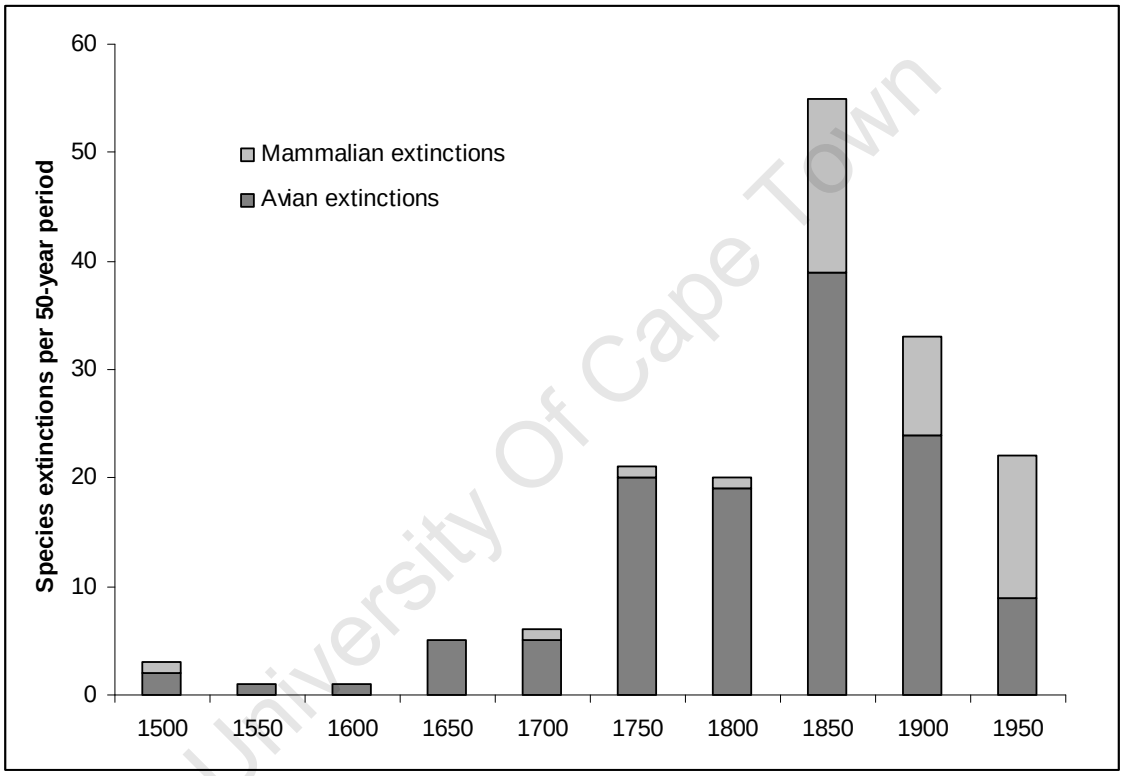

Figure 1. 50-year extinction patterns in birds and mammals from 1500.

A comparison of distributions of extinction patterns at a broad scale showed similarities and some differences among birds and mammals (Fig. 2). Among birds, the Oceanic realm recorded the highest numbers of extinctions (31%), followed by the Afrotropics (29%) and Australasia (22%). For mammals, the highest proportion of extinctions was recorded in Australasia (50%) and the Neotropics (21%).

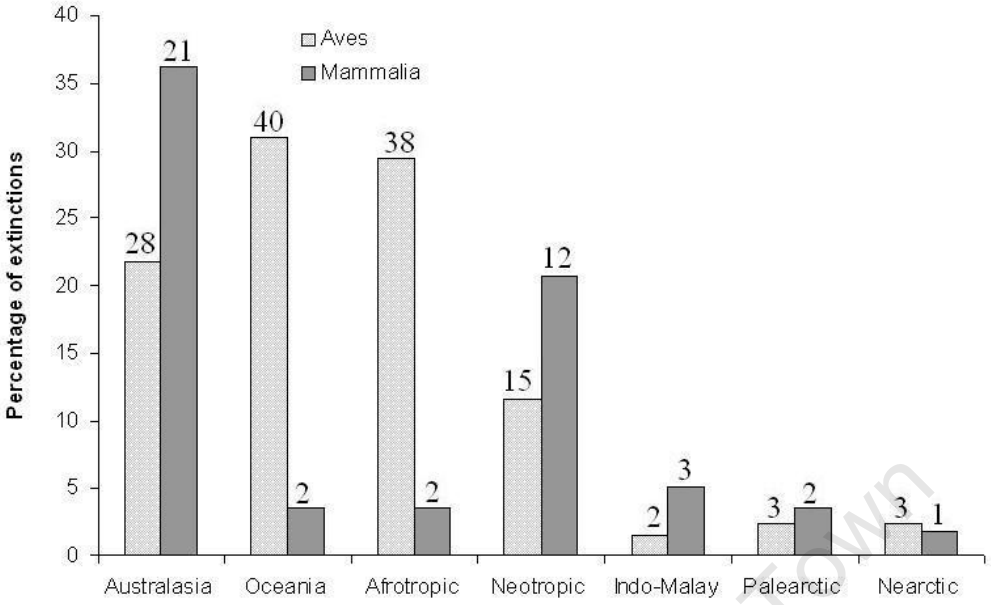

Figure 2. Distribution of avian and mammalian extinctions among the seven WWF biogeographical realms. Extinctions are given as a percentage of total extinctions for that class that occurred in each realm. Numbers of species are shown above each bar.

Regional patterns of species extinctions

An examination of patterns at a regional level shows that recent avian extinctions have occurred primarily in the Pacific islands (39 species or 30% of total avian extinctions), and the Mascarene Islands (26 species or 20% of total avian extinctions) (Fig. 3). The Pacific islands contributing to this total are the Cook Islands, Micronesia, Fiji, French Polynesia, Hawaii, New Caledonia, the Solomon Islands and Vanuatu. Hawaii and French Polynesia contribute the most to the total with 19 and 11 avian extinctions, respectively. Recent mammalian extinctions have been recorded predominantly in Australia (16 species or 38% of total mammalian extinctions). In comparison to birds, mammal extinctions in the Pacific were only 14% of the total and those in the Mascarene Islands only 2%.

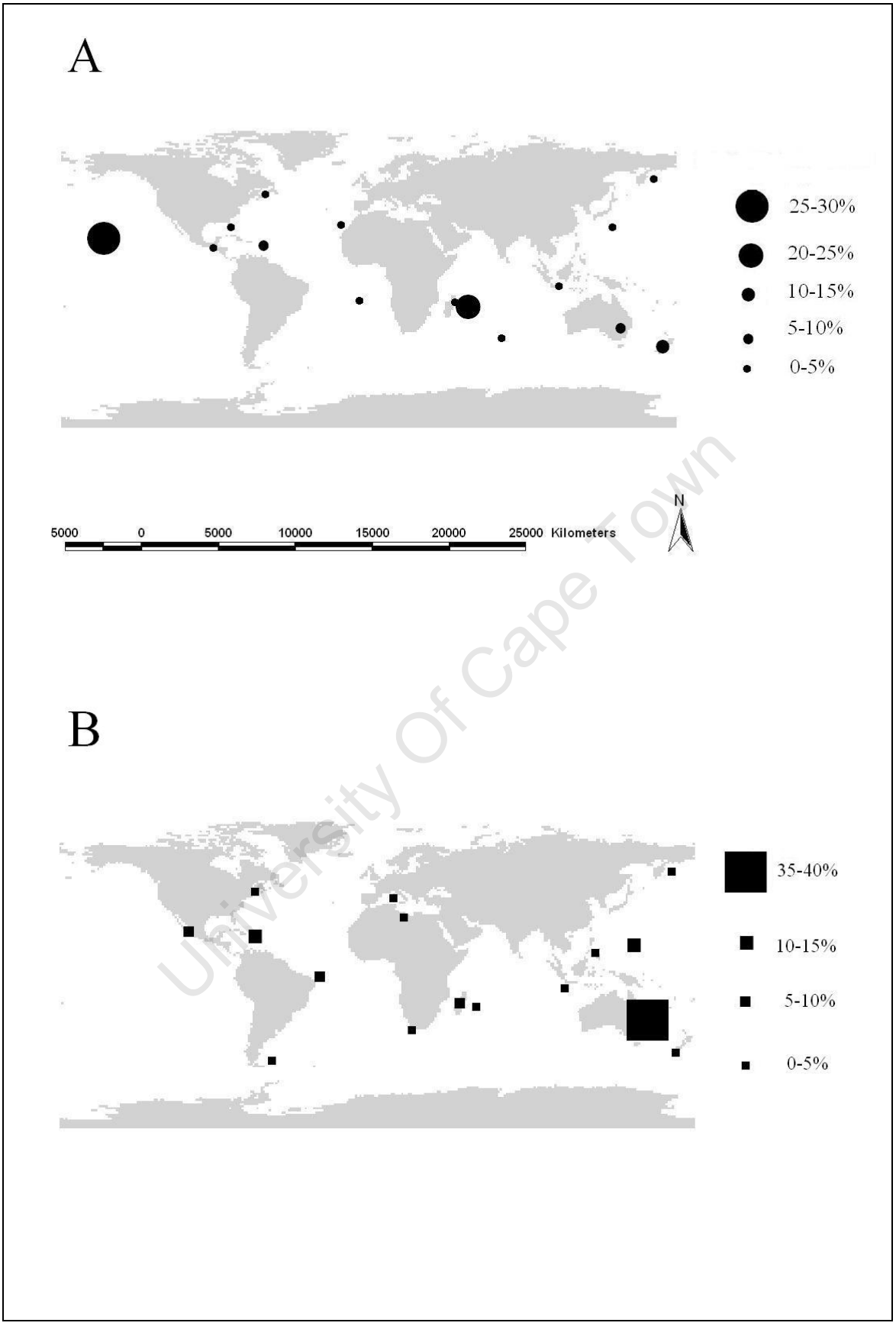

Figure 3. The global distribution of avian (A) and mammalian (B) extinctions in various regions of the world between 1500 and 2000. Symbols show the proportions of total extinctions that occurred in each region.

Temporal patterns of recent species extinction

At the global and regional scales, mammals and bird extinctions differed slightly in their patterns of occurrence over time (Fig. 4). In the 1500s, all recorded extinctions in both groups occurred in the Afrotropic and Neotropic relams. Of these, all three of the avian extinctions were recorded in the Afrotropic realm, specifically the Atlantic island of St. Helena. These species included the St. Helena Crake (*Atlantisa podarces*), the small St. Helena petrel (*Bulweria bifax*) and the St. Helena dove (*Dysmoropelia dekarchiskos*). The sole mammalian extinction that occurred during this period was of the Vespucccii's rat (*Nornhomys vespuccii*) on Brazil's Fernando de Noronha Island. In the 1600s, only six extinctions were recorded, all avian and all occurring in the Mascarene Islands (Réunion and Mauritius). In the 1700s, there was a rapid escalation in the frequency of documented extinctions among birds, but not mammals compared with the previous centuries. Avian extinctions increased to 25 with the first recorded extinctions in the Caribbean, New Zealand and Australia, the South Pacific and the North Pacific. Three mammalian extinctions were recorded in Sardinia and adjacent small islands in the Mediterranean, the Commander Islands east of Russia's Kamchatka Peninsula in the Bering Sea and the Galapagos Islands. In the 1800s, 60 bird and 17 mammal extinctions occurred. Hawaii had the highest number of recorded avian extinctions during this century (11 species). The South Pacific and the Mascarene Islands also suffered several losses (8 and 10 species, respectively). The frequency of mammalian extinctions also increased, with the first extinctions being recorded in Australasia and the South Pacific. In the 1900s, the highest numbers of avian extinctions were recorded in the South Pacific (9) and New Zealand and on Lord Howe Island (8 extinctions). Mainland Australia experienced the highest numbers of mammalian extinctions (10).

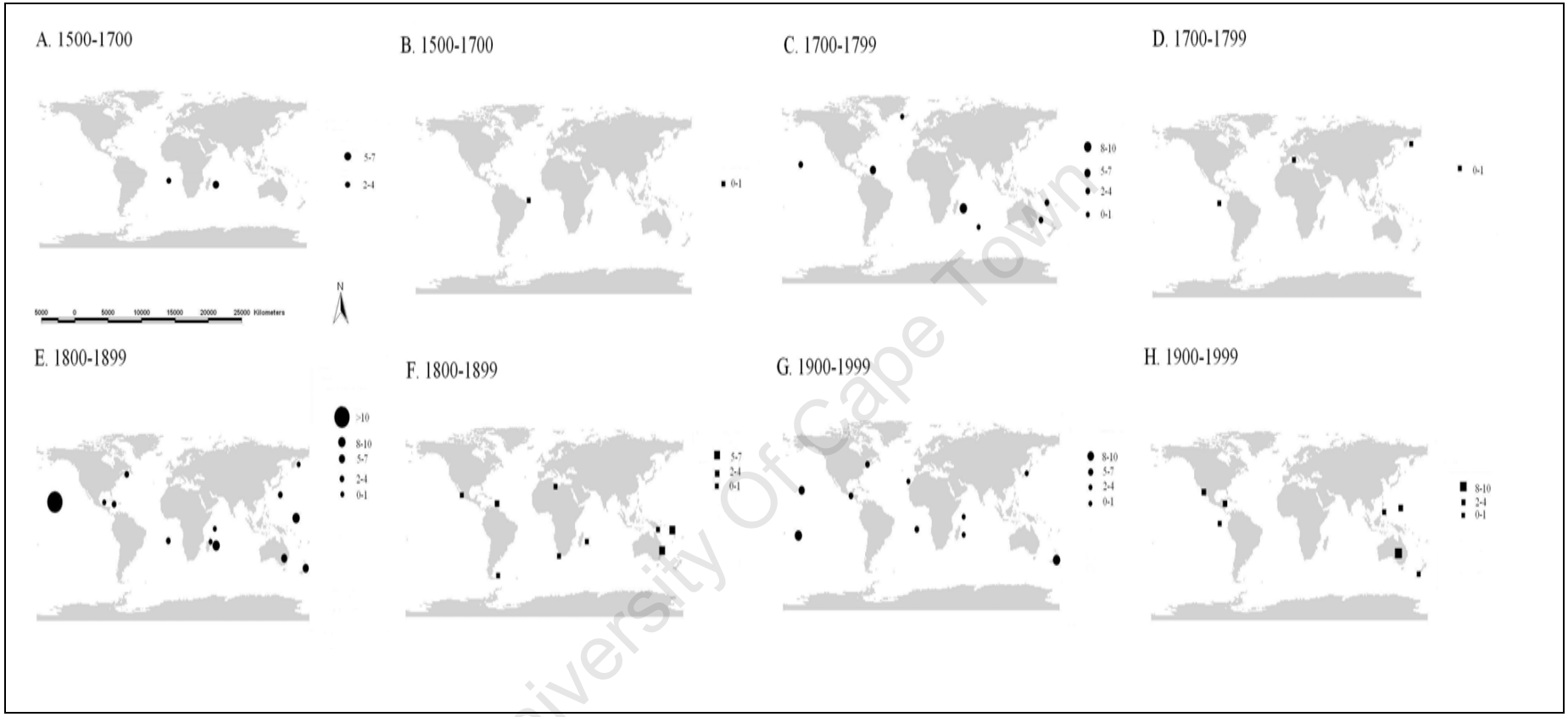

Figure 4. The global distribution of avian (A, C, E and G) and mammalian (B, D, F and H) extinctions between 1500 and 2000, by century of extinction.

Table 1. Proportions of recent avian and mammalian extinctions in each of the WWF's terrestrial biomes. Proportions are calculated as the percentage of the total extinctions in that century that in each biome

WWF Biome	Avian extinctions (%)					Mammalian extinctions (%)				
	1500-1599	1600-1699	1700-1799	1899-1899	1900-1999	1500-1599	1600-1699	1700-1799	1800-1899	1900-1999
Tropical and subtropical moist broadleaf forests	0	100	84	63	60	65	0	0	41	18
Temperate broadleaf and mixed forests	0	0	8	12	14	0	0	0	12	14
Tropical and subtropical dry broadleaf forests	0	0	0	7	3	17	0	0	12	18
Tropical and subtropical grasslands and shrublands	100	0	0	3	9	0	0	0	6	0
Temperate grasslands savannas and shrublands	0	0	4	3	3	0	0	0	6	0
Tropical and subtropical coniferous forests	0	0	0	3	3	6	0	0	0	0
Mediterranean forests, woodlands and scrub	0	0	0	1	3	0	0	50	6	18
Mangroves	0	0	0	3	0	6	0	0	0	0
Boreal forests/taiga	0	0	4	3	0	0	0	0	0	0
Temperate coniferous forests	0	0	0	0	3	0	0	0	0	0
Montane grasslands and shrubland	0	0	0	0	3	0	0	0	0	0
Deserts and xeric shrublands	0	0	0	0	0	6	0	50	18	32
Flooded grasslands and savannas	0	0	0	0	0	0	0	0	0	0
Tundra	0	0	0	0	0	0	0	0	0	0
Total	100	100	100	100	100	100	0	100	100	100

At the biome level, tropical and subtropical moist broadleaf forests experienced the greatest numbers of avian and mammalian extinctions throughout the timeframe of this analysis (Table 1). Sixty-six percent of all avian extinctions and 36% of all mammalian extinctions occurred in this biome. For mammals, desert and xeric shrublands have also experienced a relatively high number of mammalian extinctions (20%), this figure being influenced by the high numbers of arid-zone species that became extinct in Australia.

Body-mass distributions of extinct taxa

Mammals and birds showed different body-mass distributions among extinct species when compared with body-mass distributions of extant species. The mean body-mass of extant bird species is 44.7 g (Fig. 5). This is lower, but not substantially, than the value of 53.2 g reconstructed from Blackburn & Gaston, 1994; the discrepancy is likely due to inaccuracy in re-constructing the data from figure 1 in Blackburn & Gaston, *op. cit*. The mean body-mass of extinct bird species calculated from this study is 157.4 g. The frequency distribution of body-masses of the extant birds is skewed to the left (Kolmogorov D = 0.109, $P < 0.2$) (indicating a predominance of smaller taxa.), while the distribution of body-masses of extinct bird species does not differ significantly from normality (Kolmogorov D = 0.083, n.s) indicating that majority of extinct bird species were larger in body size than extant species.

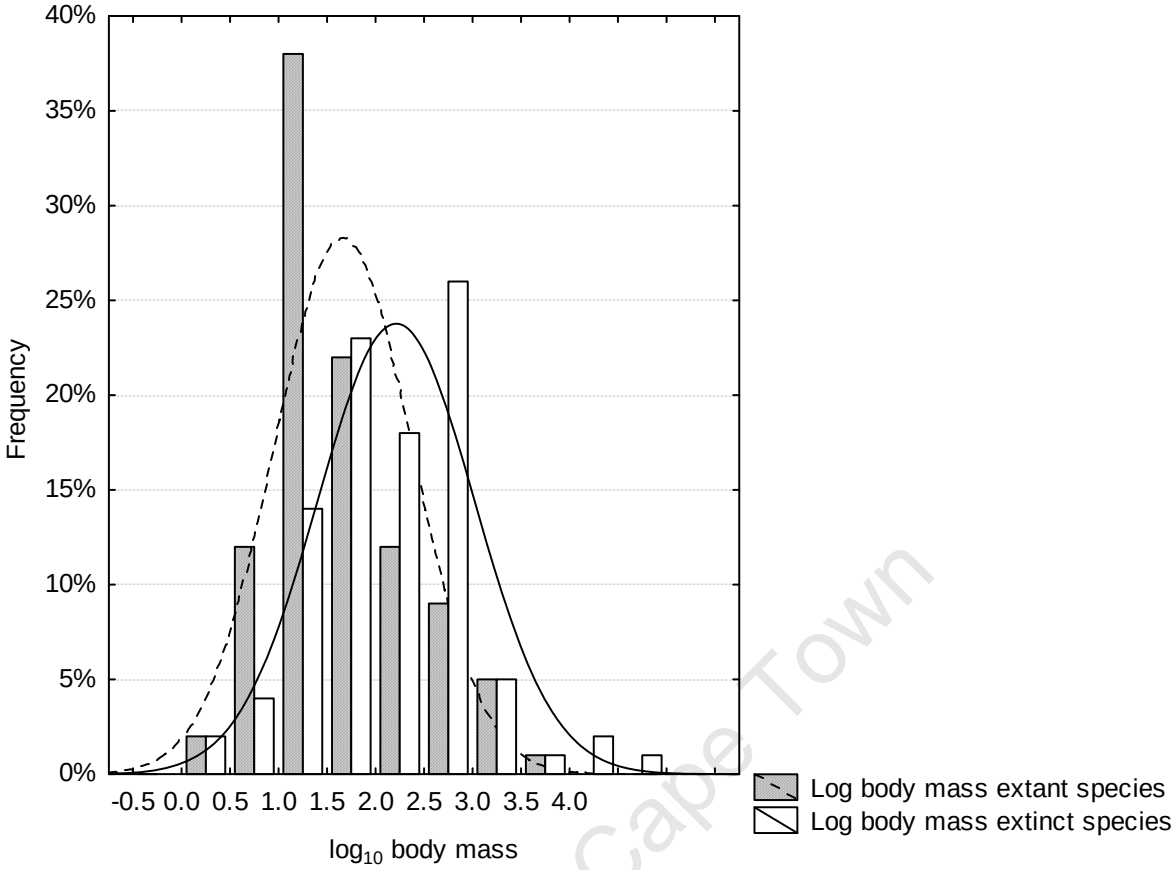

Figure 5. The percentage frequency distribution of the logarithms of body-mass for 6209 extant bird species (from Blackburn & Gaston, 1994) compared with the logarithms of body-mass of 96 extinct bird species for which body-mass is known. Body-masses were log_{10} transformed.

A global body-mass frequency distribution could not be obtained for mammals and, therefore, existing body-mass distributions constructed for North America and South America were used (re-constructed from Brown & Nicoletto, 1991 and Bakker & Kelt, 2000, respectively - Figure 9). Whilst it is unknown how these compare with global body-size distributions, continental-level body size distributions among birds are similar to the global body-size distribution among birds (Blackburn & Gaston, 1994).

Average body mass among extant mammals in the Americas falls somewhere between 100.7 g and 130.3 g. The average mass of extinct species is much higher, at 848.9 g.

The frequency distributions of extant species are skewed towards smaller species (Kolmogorov D = 0.149, $P < 0.15$ for North American species; D = 0.151, $P < 0.15$ for South American species - Figure 9). The distribution of extinct species does not differ significantly from normality (D = 0.138, $P > 0.2$) confirming that extinctions have been biased towards relatively large species. The pattern of non-random extinction with respect to body size is thus similar in birds and mammals with recently extinct species being larger on average, than a sample of extant species.

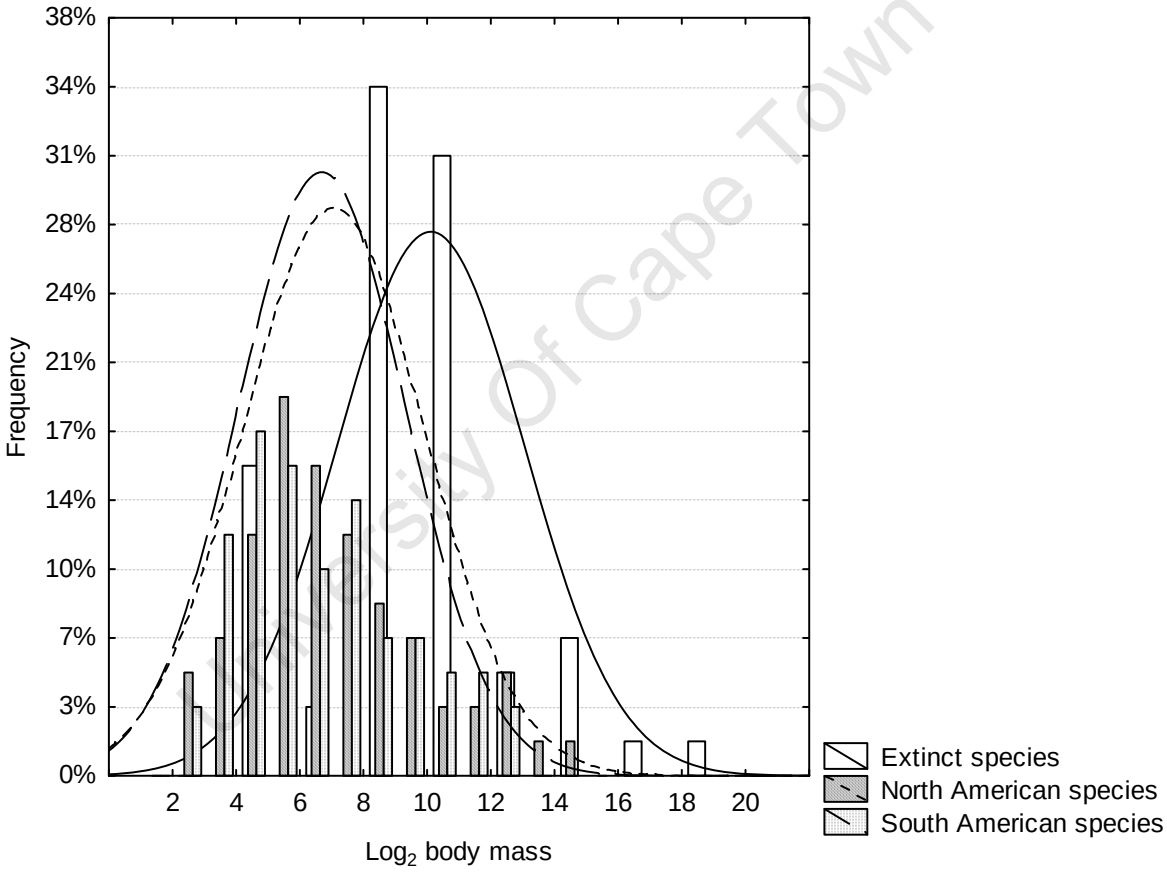

Figure 6. Body size percentage frequency distributions for the mammals of North America (*n* = 460), and South America (*n* = 720) (adapted from Brown & Nicoletto, 1991; Bakker & Kelt, 2000) compared with the body size distribution of 42 extinct mammal species. Body-masses were log_2 transformed.

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Chapter 4: Discussion

Temporal patterns of species extinctions

The peak in species extinctions between the late 1800s and the early 1900s (for both mammals and birds) is a pattern most likely driven by European expeditions into previously unknown regions during that time. The pattern may reflect the reality of extinction or merely an increase in the numbers of described species during that time because the rate at which new bird and mammal species were described also peaks at around that same time. For example, most of the over 9000 species of birds were described before the beginning of the 20th Century (Blackburn & Gaston, 1994) while the peak for mammalian species descriptions was in the mid-1800s and early-1900s (Reeder et al., 2007).

Spatial patterns of recent extinctions

If extinction risk is randomly apportioned across taxa, patterns of species richness will influence patterns of extinction with areas supporting high species richness experiencing the highest absolute extinction rates. Alternatively, if range-restricted species (localised endemics) are disproportionately impacted, the same pattern may not hold. Species richness and endemism are influenced by different factors resulting in differing patterns between the two. For example, amongst mammals, species richness is determined by size of the landmass, latitude and diversity of habitats while endemism is shaped by evolutionary and biogeographic factors (Ceballos & Brown, 1995). This study found that species endemism but not necessarily species richness, was an important predictor of extinction patterns in both birds and mammals.

At the level of the realm, avian extinctions were found to be highest in Oceania, the Afrotropics and Australasia while mammalian extinctions were highest in Australasia and the Neotropics. The Neotropics support the world's highest diversity of mammal species and the second highest diversity of genera in the world (Cole *et al.*, 1994). The realm also has a high level of mammalian endemism (82%). The Australasian realm on the other hand, supports only 10% of the world's mammal species (Cole *et al., op cit.*). However, species endemism in the region is high (89%) as is the mammalian extinction rate (21 species). The Afrotropics have experienced relatively few mammal extinctions despite having the highest levels of species endemism of all the biogeographic regions (Cole *et al., op cit.*). Underlying factors generating this pattern in the Afrotropics may be pre-historic in nature involving extinction filters removing specialised and range-restricted species prior to 1500 (Fritz *et al.*, 2008). Islands often exhibit high rates of species endemism compared to continental landmasses (Adler, 1992). The islands occurring in the Afrotropics are relatively depauperate in their mammalian fauna hence the lower rates of extinction among mammals in the realm (Adler, 1994).

At a regional scale, the Pacific islands and the Mascarene Islands have experienced the highest numbers of avian extinctions. Together, they largely account for the high extinction rates in the Oceanic and Afrotropic realms. While not particularly species rich in avifauna in comparison with other regions in the study, these areas have high levels of species endemism within islands and island groups (for example Mauritius, Réunion, Rodrigues and the Seychelles all have greater than 53% endemism; Adler, 1992, Adler, 1994). The Pacific islands, which experienced a greater number of avian extinctions, have much higher species diversity and endemism relative to the Indian Ocean islands (Adler, 1994).

At the level of the biome, avian extinctions have been shown to be tied primarily to tropical and subtropical moist forests. Mammalian extinctions, on the other hand, occurred primarily in both these habitats and in deserts and mesic shrublands. Tropical regions of the world have high levels of species richness and endemism due to their habitat heterogeneity and energy availability (Davies et al, 2007). The high mammal extinction rates in deserts and xeric shrublands are strongly influenced by the high numbers of extinctions among arid-zone species in continental Australian. Australia has high levels of species richness and endemism, on a regional and continental scale. At species level, mammals are 73% endemic and birds are 70% endemic (Common & Norton, 1992).

Body-mass and extinction

Studies of the influence of body size on extinction risk in birds and mammals have variously found either a positive, negative or no relationship in birds and mammals. Some studies have shown that currently threatened mammals (Cardillo & Bromham, 2001; Cardillo *et al.*, 2005) and birds (Blackburn & Gaston, 1995) are, on average, larger than non-threatened taxa, mirroring the pattern of past extinctions being biased towards larger-than-average taxa (Figures 5,6). Others have found that body size may be a surrogate for other ecological factors underlying extinction, such as reproductive output (Cardillo, 2003), in the same way that latitude is often used as a surrogate for ecological or life-history traits. Large body size has been associated with extinction risk because of: a) the negative relationship between body size and abundance (Damuth, 1981) although some studies have concluded that species of intermediate body size have the highest abundances (e.g., Gaston, 1994), b) the decrease in intrinsic rate of population increase with increasing body-mass (Fenschel, 1974), and c) the

disproportionate effect that human exploitation has had on large-bodied species (Jerozolimski & Peres, 2004).

The results of this study indicate that extinct species of birds and mammals were, on average, larger that extant species. This may be the result of the interaction between body size and the factors mentioned above. Over-exploited taxa were most likely large and species found on islands that had not previously experienced human colonisation and which, as a result had not evolved appropriate defence strategies against predators. In Australia, a set of different factors are thought to have interacted, causing the extinction mainly of intermediate-sized species. Morton (1990) has hypothesized that the extinction of intermediate-sized species is most likely caused by a combination of several factors including the introduction of the rabbit (*Oryctolagus cuniculus)*, an exotic species which competed with medium-sized native herbivores for habitat in already variable conditions, and the spread of the fox, (*Vulpes vulpes)*, which preyed on medium-sized mammals. Because of the interaction between body size and life-history parameters, the body-mass distribution of extinct species is not likely to change in future despite habitat loss and invasive species having replaced over-exploitation as the primary causes of extinction (IUCN, 2009).

Causes of recent extinctions in mammals and birds

Habitat loss, invasive species and over-exploitation have been identified as the most important factors to have caused avian and mammalian extinctions since 1500 (Bibby, 1994; Clavero & Garcia-Berthou, 2005). These causes are reflected in patterns of recent extinctions of birds and mammals. Over-exploitation is most likely to have impacted larger species of birds and mammals as shown by the body size distributions of recently extinct mammal and bird species. Introductions of mammalian species have caused

extinctions of many oceanic island birds particularly on islands with no native mammal predators, where native birds had not evolved appropriate anti-predator defences to escape predation (e.g., McChesney & Tershy, 1998). A well-documented example of the impacts of an introduced mammal is that of *Rattus rattus*, which is thought to have been responsible for the extinctions of nine native species of landbirds, the last surviving population of the greater short-tailed rat (*Mystacina robusta*), and at least one species of flightless weevil following its introduction on New Zealand's Big South Cape Island in the 1960s (references?).

Introduced mammalian species can also have a severe impact on native mammal species. The introduction of *R. rattus* is thought to be responsible for the extinctions of all six species of endemic rice-rats on the Galapagos Islands (Amori & Clout, 2003). The impact of introduced rodent species has most likely been through competition with native species (Amori & Clout *op.cit.*). A large proportion of recently extinct mammals in this study were rodents, pointing to the potential impacts of competition by introduced rodents on native rodents. Endemic species are particularly vulnerable to the impacts of invasive species (Blackburn *et al*., 2004), and as shown by results in the present study, islands with high endemism of birds and mammals recorded the highest numbers of extinctions.

Can the patterns found among birds and mammals inform us about risks facing less well-known taxa such as reptiles and amphibians? Although there have been relatively few recent reptile extinctions in the last 500 years compared with birds and mammals (Case et al., 1998), extinction patterns in reptiles are most likely to be similar to those of birds (but not necessarily mammals) for a number of reasons (from an analysis of Holocene extinction patterns among reptiles by Case et al., *op. cit.*):

- All recent extinctions among reptiles have occurred on islands, which are thought to have a reptile species richness comparable to that of birds and greater than that of mammals
- Invasive species are thought to be an important factor interacting with habitat loss to elevate reptile extinction rates. This impact was found to come mainly from predation by exotic mammals such as mongooses rather than competition by exotic reptiles. This suggests that reptile extinction patterns would be similar to those of birds, for which predation by exotic mammals has been an important factor in predicting extinction risk.

Of the 5743 described species of amphibians, 34 have become extinct since 1500, but nine of these have occurred since 1980, indicating that the situation may be worsening (Stuart *et al*., 2004). Geographic patterns of amphibian extinctions differ from those of birds, mammals or reptiles, with the majority of recent amphibian extinctions occurring among Neotropical, montane, stream-associated species (Stuart et al., op.cit.). These areas have high species richness and endemism, as do islands in comparison to continental areas of comparable size (Duellman, 1999). A complex interaction of factors is thought to be causing these declines including over-exploitation, land-use change, invasive species, UV radiation from climate change, toxic chemicals and emerging infectious diseases such as chytridiomycosis (Collins & Storfer, 2003). The latter two factors are thought to be particularly important in very recent amphibian declines. Patterns of recent amphibian extinctions will most likely differ from both birds and mammals due to the differences in underlying factors causing these extinctions.

Conclusions

Overall, patterns of recent extinctions in mammals and birds reflected patterns of endemism and the nature of the impact. For both birds and mammals, species endemism was an important factor in predicting areas where recent extinctions occurred. Body size was also a good predictor of extinction, with the majority of recently extinct species having been larger on average than a global sample of bird or mammal species. The influence of body size is most likely due to the role of human exploitation in recent extinctions, although other factors causing extinction (e.g., the impact of invasive species in Australia) also showed size-selectivity in extinction impact due to the nature of the impact (affecting intermediate-sized mammals disproportionately). The patterns have also shown invasive species to be of particular importance in recent extinctions among both mammals and birds, impacting endemic species by preying on naïve bird species and competing with native mammal species, leading to their extinction. The results of this study may be able to inform us about reptiles but not necessarily about amphibian patterns of extinction as reptile extinctions have generally followed similar trends and been caused by similar factors as birds. However for amphibian extinctions, the interaction of multiple factors in recent amphibian declines may mask general patterns of extinction that may be similar to those of other taxa.

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Appendices

Appendix 1: Sources of data for body-masses of recently extinct mammals

Species	Source, body-mass
Brotomys voratus	Masses of other echimyidae (*Proechymys semipinosus, P. guyannensis, P. guairae*) from O' Connell, 1986
Caloprymnus campestris	Geiser & Turnbill, 2009
Chaeropus ecaudatus	Strahan, 1988
Conilurus albipes	Smith & Quin, 1996
Dobsonia chapmani	Pteropodidae Kuzler, 1990
Dusicyon australis	Naaktegeboreen, 1990
Gazella rufina	Geiser & Turbill, 2009
Geocapromys thoractus	*G. ingrahami* in Stahke & Hendricks. 1990
Geocapromys columbianus	*G. ingrahami* in Stahke & Hendricks. 1990
Hexolobodon phenax	*Plagiodontia aedium* in Stahke & Hendricks, 1990
Hippopotamus lemerei	Geiser & Turbill, 2009
Hippotragus leucophaeus	Klein, 1974
Hydrodamalis gigas	Geiser & Turbill, 2009
Isolobodon montanus	*Plagiodontia aedium* in Stahke & Hendricks, 1990
Isolobodon portoricensis	*Plagiodontia aedium* in Stahke & Hendricks, 1990
Lagorchestes asomatus	Ganslosser, 1990
Lagorchestes leporides	Strahan, 1988
Leporillus aplicalis	Geiser & Turbill, 2009
Macropus greyi	Ganslosser, 1990
Macrotis leucura	Schneider, 1990
Megaladapis edwardsi	Geiser & Turbill, 2009
Megalomys luciae	Geiser & Turbill, 2009
Megalomys desmerestii	Geiser & Turbill, 2009
Megaoryzomys curioi	Geiser & Turbill, 2009
Monachus tropicalis	Schliemann, 1990
Mustela macrodon	Geiser & Turbill, 2009
Mystacina robusta	*Mystacina* sp O'Donnell *et al.*, 1999
Nesophontes hypomicrus	Barcley & Harder, 2005
Nesophontes paramicrus	Barcley & Harder, 2005
Nesophontes zamicrus	Barcley & Harder, 2005
Nesophontes superstes	Barcley & Harder, 2005
Nesoryzomys darwinii	Geiser & Turbill, 2009
Noronhomys vespucii	Geiser & Turbill, 2009
Notomys longicaudatus	Dieterlen, 1990
Notomys amplus	Dieterlen, 1990
Nyctimene sanctacrucis	Pteropodidae Kuzler, 1990
Oligoryzomys victus	Congeners *O. nigripes, O. chacoensis* and *O. eliurus* in Caseres *et al.*, 2007
Onychogalea lunata	Ganslosser, 1990
Oryzomys nelsonii	*O. palustris* Niethammer, 1990
Oryzomys antillarum	*O. palustris* Niethammer, 1990
Palaeopropithecus ingens	Extant species from sister taxon *Propithecus diadema* and *P. verrauxi* from Kolar, 1990
Perameles eremiana	Schneider, 1990
Peromyscus pembertoni	Geiser & Turbill, 2009
Pharotis Imogene	Kuzler, 1990

Plagiodontia ipnaeum	*P. aedium* in Stahke & Hendricks, 1990
Potorous platyops	Ganslosser, 1990
Prolagus sardus	Geiser & Turbill, 2009
Pseudomys gouldii	Dieterlen, 1990
Pteropus subniger	Masses of *Pteropus* sp. From Barcley & Harder, 2005, Kuzler, 1990
Pteropus tokudae	Masses of *Pteropus* sp. From Barcley & Harder, 2005, Kuzler, 1990
Pteropus pilosus	Masses of *Pteropus* sp. From Barcley & Harder, 2005, Kuzler, 1990
Pteropus brunneus	Masses of *Pteropus* sp. From Barcley & Harder, 2005, Kuzler, 1990
Rattus macleari	Masses of congeners *R. rattus* and *R. norweigicus* from Dieterlen, 1990
Rattus nativatis	Masses of congeners *R. rattus* and *R. norweigicus* from Dieterlen, 1990
Rhizoplagiodontia lemkei	Geiser & Turbill, 2009
Solenodon macranoi	Masses of congeners *S. paradoxus* and *S. cubanus* from Fons, 1990
Sylvilagus insonus	Geiser & Turbill, 2009
Thylacinus cynocephalus	Moeller, 1990
Uromys porculus	Dieterlen, 1990
Uromys imperator	Dieterlen, 1990
Xenothrix mcgregori	Masses of other Callicebinae *Callicebus moloch, C. torquatus*, and *C. personatus* from Witt, 1990

Appendix 2: Estimated Extinction Dates (EED) and body-masses for mammals

Species	Common name	EED	Body-mass (g)
Brotomys voratus	Hispaniolan Spiny Rat	1500	335
Geocapromys columbianus	Columbian Hutia	1500	800
Hexolobodon phenax	Imposter Hutia	1500	2000
Hippopotamus lemerei	Malagasy Dwarf Hippopotamus	1500	420000
Isolobodon montanus	Montane Hutia	1500	2000
Isolobodon portoricensis	Puerto Rican Hutia	1500	2000
Megaladapis edwardsi	Tretretretre	1500	20000
Nesophontes hypomicrus	Atalaye Nesophont	1503	500
Nesophontes paramicrus	Saint Michel Nesophont	1500	500
Nesophontes superstes	Victorious Nesophont	1500	500
Nesophontes zamicrus	Haitian Nesophont	1500	500
Palaeopropithecus ingens	Large Sloth Lemur	1500	6500
Plagiodontia ipnaeum	Samana Hutia	1500	2000
Rhizoplagiodontia lemkei	Lemke's Hutia	1500	2000
Solenodon marcanoi	Marcano's Solenodon	1500	800
Xenothrix mcgregori	Jamaican Monkey	1500	1000
Noronhomys vespuccii	Vespucci's Rat	1503	2500
Megaoryzomys curioi	Curio's Giant Rat	1740	2500
Hydrodamalis gigas	Steller's Sea Cow	1768	400000
Prolagus sardus	Sardinian Pika	1777	250
Hippotragus leucophaeus	Bluebuck	1800	180000
Mustela macrodon	Sea Mink	1860	1400
Pteropus subniger	Réunion Flying Fox	1860s	760
Pteropus brunneus	Percy Island Flying Fox	1874	760
Pteropus pilosus	Large Palau Flying Fox	1874	760
Conilurus albipes	White-footed Rabbit-Rat	1875	
Potorous platyops	Broad-faced Potoroo	1875	1230
Dusicyon australis	Falkland Islands Wolf	1876	51000
Oryzomys antillarum	Jamaica Rice-rat	1877	60
Megalomys luciae	St. Lucia Giant Rice-rat	1881	60
Uromys porculus	Guadalcanal Rat	1887	850
Lagorchestes leporides	Eastern Hare-wallaby	1890	2850
Pharotis imogene	New Guinea Big-eared Bat	1890	28
Nyctimene sanctacrucis	Nendo Tube-nosed Fruit Bat	1892	500

Oligoryzomys victus	St. Vincent Pygmy Rice-rat	1892	25
Gazella rufina	Red Gazelle	1804	14000
Notomys amplus	Short-tailed Hopping Mouse	1896	35
Oryzomys nelsoni	Nelson's Rice-rat	1897	60
Notomys longicaudatus	Long -tailed Hopping Mouse	1901	35
Megalomys desmarestii	Martinique Giant Rice-rat	1902	2500
Rattus macleari	Maclear's Christmas Island Rat	1903	280
Rattus nativitatis	Bulldog Rat	1903	280
Pseudomys gouldii	Gould's Mouse	1930	50
Peromyscus pembertoni	Pemberton's Deer Mouse	1931	60
Caloprymnus campestris	Desert Rat-kangaroo	1932	1150
Thylacinus cynocephalus	Thylacine	1936	25000
Nesoryzomys darwini	Darwin's Galapagos Mouse	1940	2500
Chaeropus ecaudatus	Pig-footed Bandicoot	1950s	500
Geocapromys thoracatus	Swan Island Hutia	1950s	800
Monachus tropicalis	Carribean Monk Seal	1950s	16000
Onychogalea lunata	Crescent Nailtail Wallaby	1956	7000
Lagorchestes asomatus	Central Hare-wallaby	1960s	2850
Macrotis leucura	Rabbit-eared Bandicoot	1960s	1400
Perameles eremiana	Desert Bandicoot;	1960s	1200
Uromys imperator	Emperor Rat	1960s	850
Mystacina robusta	New Zealand Greater Short-tailed Bat		30
Pteropus tokudae	Guam Flying Fox	1968	760
Dobsonia chapmani	Negros Naked-backed Fruit Bat	1970s	550
Leporillus apicalis	Lesser Stick-nest Rat	1970	60
Macropus greyi	Toolache Wallaby	1972	20900
Sylvilagus insonus	Omilteme Cottontail	1991	700

Appendix 3: Estimated Extinction Date (EED) and body-mass for birds

Species	**Common name**	**EED**	**Body-mass (g)**
Alectroenas nitidissima	Mauritius Blue-Pigeon	1828	?
Alectroenas rodericana	Rodrigues Blue-Pigeon	1738	350
Alopochen kervazoi	Reunion Shelduck	1698	2600
Alopochen mauritianus	Mauritius Shelduck	?	2600
Amazona martinicana	Martinique Amazon	1698	?
Amazona violacea	Guadeloupe Amazon	1775	?
Anas marecula	Amsterdam Duck	1795	700
Anas theodori	Mauritius Duck	1793	700
Anthornis melanocephala	Chatham Island Bellbird	1703	?
Aphanapteryx bonasia	Red Rail	1906	?
Aphanapteryx leguati	Rodrigues Rail	1697	?

Aplonis corvina	Kosrae Starling	1744		60
Aplonis fusca	Norfolk Island Starling	1854		60
Aplonis mavornata	Mysterious Starling	1921		60
Ara atwoodi	Dominican Green-and-yellow Macaw	1900		800
Ara erythrocephala	Jamaican Green-and-yellow Macaw	1799		800
Ara gossei	Jamaican Red Macaw	1847		800
Ara guadeloupensis	Lesser Antillean Macaw	1790		800
Ara tricolor	Cuban Macaw	1760		800
Aratinga labati	Guadeloupe Parakeet	1853		120
Argusianus bipunctatus	Double-banded Argus	1775	?	
Atlantisia podarces	St Helena Crake	1871	?	
Bowdleria rufescens	Chatham Island Fernbird	1502		35
Bulweria bifax	Small St Helena Petrel	1900	?	
Cabalus modestus	Chatham Island Rail	1550	?	
Caloenas maculata	Liverpool Pigeon	1899	?	
Camptorhynchus labradorius	Labrador Duck	?	?	
Caracara lutosa	Guadalupe Caracara	1877	?	
Chaetoptila angustipluma	Kioea	1900		30
Chaunoproctus ferreorostris	Bonin Grosbeak	1850		56
Chloridops kona	Kona Grosbeak	1859	?	
Chlorostilbon bracei	Brace's Emerald	1894		3
Chlorostilbon elegans	Gould's Emerald	1878		3
Ciridops anna	Ula-ai-hawane	1861		20
Columba duboisi	Reunion Pigeon	1915		350
Columba jouyi	Ryukyu Wood- Pigeon	1725		350
Columba versicolor	Bonin Wood-Pigeon	1920		350
Conuropsis carolinensis	Carolina Parakeet	1889	?	

Coturnix novaezelandiae	New Zealand Quail	1920	100
Coua delalandei	Snail-eating Coua	1875	160
Cyanoramphus ulietanus	Raiatea Parakeet	1834	70
Cyanoramphus zealandicus	Black-fronted Parakeet	1879	70
Diaphorapteryx hawkinsi	Hawkins's Rail	1842	?
Drepanis funerea	Black Mamo	1907	20
Drepanis pacifica	Hawaii Mamo	1899	20
Dromaius ater	King Island Emu	1802	40,000
Dromaius baudinianus	Kangaroo Island Emu	1827	10000
Dysmorodrepanis munroi	Lanai Hookbill	1920	20
Dysmoropelia dekarchiskos	St Helena Dove	1502	?
Ectopistes migratorius	Passenger Pigeon	1900	200
Falco buboisi	Réunion Kestrel	1672	?
Fregilupusvarius	Réunion Starling	1855	80
Fulica newtoni	Mascarene Coot	1683	?
Gallicolumba ferruginea	Tanna Ground-Dove	1774	130
Gallicolumba norfolciensis	Norfolk Island Ground-Dove	1802	130
Gallicolumba salamonis	Thick-billed Ground-Dove	1927	130
Gallinula nesiotis	Tristan Moorhen	1890	?
Gallirallus dieffenbachii	Dieffenbach's Rail	1872	150
Gallirallus pacificus	Tahiti Rail	1930	150
Gallirallus wakensis	Wake Island Rail	1944	150
Gerygoneinsularis	Lord Howe Island Gerygone	1936	<10
Haematopus meadewaldoi	Canary Islands Oystercatcher	1960	600
Hemignathus ellisianus	Greater Akialoa	1860	10
Hemignathus obscurus	Lesser Akialoa	1940	10
Hemignathus sagittirostris	Greater Amakihi	1901	10

Heteralocha acutirostris	Huia	1907		225
Ixobrychus novaezelandiae	Black-backed Bittern	1900		150
Lophopsittacus bensoni	Mauritius Grey Parrot	1799		250
Lophopsittacus mauritianus	Broad-billed Parrot	1675		250
Mascarenotus grucheti	Réunion Owl	1620		550
Mascarenotus murivorus	Rodrigues Owl	1726		550
Mascarenotus sauzieri	Mauritius Owl	1837		550
Mascarinus mascarinus	Mascarene Parrot	1790	?	
Mergus australis	Auckland Islands Merganser	1902		1000
Microgoura meeki	Choiseul Pigeon	1905	?	
Moho apicalis	Oahu O'o	1860		30
Moho bishopi	Bishop's O'o	1893		30
Moho braccatus	Kauai O'o	1855		30
Moho nobilis	Hawaii O'o	1786		30
Mundia elpenor	Ascension Flightless Crake	?		38
Myadestes myadestinus	Hawaiian Thrush	1887		80
Myadestes woahensis	Amaui, 'amaui	1825		80
Myiagra freycineti	Guam Flycatcher	1881	?	
Nannococcyx psix	St Helena Cuckoo	1875	?	
Necropsar rodericanus	Rodrigues Starling	1879		80
Necropsittacus rodericanus	Rodrigues Parrot	1867		250
Nesillas aldabrana	Aldabra Brush-Warbler	1968	<10	
Nesoclopeus poecilopterus	Bar-winged Rail	1866	?	
Nestor productus	Norfolk Island Kaka	1836	?	
Nycticorax duboisi	Reunion Night-Heron	1907		900
Nycticorax mauritianus	Mauritius Night-Heron	1893		900
Nycticorax megacephalus	Rodrigues Night-Heron	1873		900

Paroreomyza flammea	Kakawahie	1889	11
Pezophaps solitaria	Rodrigues Solitaire	1789	25000
Phalacrocorax perspicillatus	Pallas's Cormorant	1811	1900
Pinguinus impennis	Great Auk	1758	2000
Podiceps andinus	Colombian Grebe	1959	400
Podilymbus gigas	Atitlán Grebe	1929	500
Pomarea fluxa	Eiao Monarch	1977	?
Pomarea mira	Ua Pou Monarch	1985	?
Pomarea nukuhivae	Nuku Hiva Monarch	1975	?
Pomarea pomarea	Maupiti Monarch	1828	?
Porphyri oalbus	White Gallinule	1790	800
Porphyrio coerulescens	Réunion Gallinule	1848	800
Porphyrio kukwiedei	New Caledonia Gallinule	1989	800
Porphyrio mantelli	North Island Takahe	1848	800
Porzana astrictocarpus	St Helena Rail	1973	60
Porzana monasa	Kosrae Crake	1858	60
Porzana nigra	Miller's Rail	1784	60
Porzana palmeri	Laysan Rail	1892	60
Porzana sandwichensis	Hawaiian Rail	1789	60
Prosobonia ellisi	White-winged Sandpiper	1906	36
Prosobonia leucoptera	Tahitian Sandpiper	1789	36
Psephotus pulcherrimus	Paradise Parrot	1845	60
Psittacula exsul	Newton's Parakeet	1872	120
Psittacula wardi	Seychelles Parakeet	1867	120
Pterodroma rupinarum	Large St Helena Petrel	1975	400
Ptilinopusmercierii	Red-moustached Fruit-Dove	1849	130
Quiscalus palustris	Slender-billed Grackle	1827	130

Raphus cucullatus	Dodo	1758	25000
Rhodacanthis flaviceps	Lesser Koa-Finch	1892	20
Rhodacanthis palmeri	Greater Koa-Finch	1892	20
Sceloglaux albifacies	Laughing Owl	1844	?
Sula tasmani	Tasman Booby	1928	?
Threskiornis solitarius	Réunion Flightless Ibis	1848	1200
Traversia lyalli	Stephens Island Wren	1894	16
Turdus ravidus	Grand Cayman Thrush	1886	80
Turnagra capensis	South Island Piopio	1787	?
Turnagra tanagra	North Island Piopio	1865	?
Upupa antaios	St Helena Hoopoe	1975	?
Xenicus longipes	Bush Wren	1789	16
Zoothera terrestris	Bonin Thrush	1831	80
Zosterops strenuus	Robust White-eye	1855	10